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Generic and Referential Alarm Calls Differently Alter Nest Vigilance at Dusk and Dawn in a Common Songbird

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Abstract – Prey attune to predation risk and use information obtained in the present to modify decision making into the future. Prey that produce referential alarm calls to different risks could use information from calls to alter future vigilance in threat-specific ways. Northern yellow warblers (*Setophaga aestiva*) give referential 'seet' alarm calls to denote brood parasitic brown-headed cowbirds (*Molothrus ater*) and generic 'chip' calls to predators and conspecifics around nests. We tested whether warblers differently adjust nest attendance in the future based on different alarm calls, predicting that laying females exposed to seet playbacks increase attendance at dusk and dawn (to interfere when cowbirds lay), whereas females exposed to chip playbacks generally avoid nests (so as not to reveal its location). Using camera traps, we quantified the proportion of photos with females on nests and the number of on-off bouts and combined them as nest attendance using principal components analysis. At dusk, females exposed to chip and seet calls spent a lesser proportion of time at nests than those exposed to silence, whereas at dawn females exposed to seet calls spent a greater proportion of time at nests than females exposed to chips or control. Overall, at dusk females exposed to seet calls and silence showed higher nest attendance than those exposed to chips whereas at dawn females exposed to seet calls showed higher attendance than to silence, but not chips. Female nest attendance did not differ across treatments during afternoon observations. Females used alarm calls detected during the day to adjust behavior at dusk and the next morning. Yellow warblers appeared to recall information from past encounters to modify future decisions, suggesting a potential for advanced cognition in a fitness-relevant socio-ecological context.

Keywords – Alarm calling, Brood parasitism, Episodic-like memory, Host-parasite interactions, Nest vigilance, Referential signaling, Northern yellow warblers

Prey use a variety of unimodal and multimodal cues and signals to assess and communicate predation risk (Mathot et al., 2024). The presence of direct cues, such as predators or their vocalizations, and indirect signals, such as conspecific alarm or mobbing calls, may alter behavioral and reproductive decisions, including the expression of sexual displays (e.g. de Moraes et al., 2019), allocation of paternity (e.g. Santema et al., 2019), onset and timing of incubation (Martin & Briskie, 2009), and reproductive success (Zanette et al., 2011). These long-term consequences of attuning to predation risk reveal that animals use information obtained in the present to modify behavior and decision making into the future. Information about predation risk may accrue over the breeding season influencing overall perceived risk (Lima 2009), yet it appears that even one-time or short-term exposure to predation threats to reproductive success can modify future behavior (Wegdell et al., 2019; Wheeler et al., 2019; Léon et al., 2022; see also Winiarska et al., 2024).

Alarm calls typically indicate the presence of predators and immediate predation risk (e.g., Zuberbühler, 2009; Suzuki, 2011). Generic alarm calls are produced in various social and predatory contexts, and in the latter case, act as general cues of predation risk. Some species also produce referential alarm calls, which are acoustically distinct, given to specific predators, and elicit responses from receivers that are appropriate to the type of predator, even in the absence of direct cues of the threat itself (Gill & Bierema, 2013; Townsend & Manser, 2013). The ability to discriminate between generic and referential calls may fine-tune risk assessment, allowing receivers to respond immediately in ways that may decrease predation risk to themselves and receivers (Zuberbühler, 2009). Alarm calls also could be used to modify future defensive behavior in threat-specific ways, potentially reducing vigilance costs and influencing other reproductive decisions (Lawson et al., 2021a).

Nearly 17% of avian species face the additional threat to reproductive success of obligate brood parasitism (Antonson et al., 2020). In obligate brood parasitism, female parasites lay their eggs in the nests of host species. Host females incubate parasitic eggs and care for parasitic young, which typically hatch earlier, grow more rapidly, and beg more aggressively than host young (Payne, 1977; Soler, 2014). As a result, parasitic young may acquire more food from the host parents, sometimes leading to the death of host offspring (Hauber, 2003; Antonson et al., 2025). Hosts express frontline defenses (that is, behaviors performed before nests are parasitized) more intensely during egg-laying and incubation when brood parasites pose a greater threat to reproductive success compared with nestling periods when predators elicit stronger responses (Feeney et al., 2012; Lawson et al., 2021b). During nest defense, a small number of host species produce referential alarm calls to brood parasites and generic calls to predators (Gill & Sealy, 1996; Feeney et al., 2013, 2025), providing the opportunity to explore whether alarm calls alter future behavior in threat-specific ways.

Emerging evidence exists in passerine birds for future decision making in response to threat-specific alarm calls during breeding (Lawson et al., 2021a; see also Feeney & Langmore, 2015). In North America, northern yellow warblers (*Setophaga aestiva*) are parasitized by brown-headed cowbirds (*Molothrus ater*; Sealy, 1992, 1995) and exhibit distinct responses to cowbirds compared to nest predators. They use generic 'chip' calls during territory and nest defense against conspecifics and avian and mammalian predators, increasing rate of calling from laying to nestling stages (Hobson et al., 1988, Gill & Sealy, 1996), but produce 'seet' calls primarily to brood parasitic cowbirds during egg-laying and early incubation (Hobson & Sealy, 1989; Gill & Sealy, 1996). Playbacks of seet calls alone elicit a second cowbird-specific response, that of nest-protection behavior, providing evidence that these calls are referential, denoting the presence of cowbirds (Gill & Sealy, 2004). In addition to immediate responses to playbacks, yellow warblers also alter future behavior: in response to seet calls played the previous day, incubating yellow warblers increased nest attendance at dawn the following morning (Lawson et al., 2021a), which corresponds to the time of day when cowbirds parasitize nests (Neudorf & Sealy, 1994). These results suggest that females recalled seet calls played to them the day before when making decisions about nest attendance during incubation. Cowbirds parasitize warbler nests more frequently during early egg laying (0-2 eggs) than incubation (Sealy, 1992, 1995) and considerable unexplained variation exists in dawn nest attendance by laying female warblers (Sealy et al. 2000), which could result from differences in exposure to seet calls or in interactions with cowbirds searching for host nests during daytime (typically in the late morning: Thompson, 1994). Such interactions could also affect vigilance at other times of day, but whether females exposed to seet calls alter nest attendance during the day remains unknown. Thus, testing whether and how different alarm calls alter yellow warbler vigilance during early laying when parasitism is more likely to occur and at other times of day when cowbirds are active for different reasons will increase our understanding of how nesting birds use alarm calls in decision making in the future.

We tested the hypothesis that laying yellow warblers alter future nest vigilance in threat-specific ways in response to alarm calls played at the nest. Using camera traps, we quantified nest attendance as a proxy for vigilance based on the proportion of photos with females on their nests and the number of on-off bouts, testing whether yellow warblers exposed to alarm call playbacks (chip or seet) earlier in the day altered nest attendance later in the afternoon and at dusk, as well as at dawn the following morning compared to silent controls. We predicted that yellow warblers exposed to seet calls spend more time at the

nest at dusk and at dawn the next morning to minimize the risk of parasitism, but they would not alter attendance during the afternoon. We reasoned that females increase attentiveness at dusk as an alternative pathway to dawn vigilance: roosting females spend more time on their nests during the critical period for parasitism than females that arrive at their nests at dawn (Neudorf & Sealy, 1994). Females exposed to chip calls generally avoid nests during playbacks (Gill & Sealy, 2004) and as incubation has not yet begun when we tested nests (Hébert & Sealy, 1992), we predicted that females receiving chip playbacks show lower attendance during all time periods relative to controls to minimize risk. Exploring whether exposure to different types of alarm calls alters future vigilance provides additional insight into the meaning of alarm calls and offers a window into cognitive processes associated with threat recognition and the timing of critical defensive responses.

Methods

Ethics Statement

Our project was conducted with approval from Western Michigan University's Animal Care and Use Committee (#22-01-01).

Nest Searching and Monitoring

We conducted field work in May to June 2021 and 2022, at two sites in southwest Michigan, U.S.A. One site was a restored wetland habitat within an agricultural landscape (42.2342350, -85.9343550). Northern yellow warblers nested in various small trees and shrubs, including autumn olive (*Elaeagnus umbellata*), roses (*Rosa spp.*), and raspberry brambles (*Rubus spp.*). The second was an upland habitat in a suburban matrix (42.1966890, -85.5505550), where warblers primarily nested in autumn olive and eastern red cedar (*Juniperus virginiana*). Cowbird parasitism rates on warblers at the two sites were similar (30% of 48 nests and 40% of 47 nests parasitized at wetland and upland sites, respectively (Kelly et al., unpublished data).

We visited sites every 1-2 days and searched areas where we observed females carrying nest material or chipping and staying within a small area. We checked nests every day (weather permitting) until the first or second egg was laid. Yellow warblers typically lay clutches of 4-5 eggs and begin incubating with the penultimate egg (Hébert & Sealy, 1992); therefore, we tested females on the day they laid their first (n = 27) or second egg (n = 6) before incubation began. Females were not tested if their nests were parasitized. Parasitism rates for experimental nests (30.3% of 33 nests) and those monitored but not tested (33.4% of 56 nests) were similar (X^2 = 0.12, p > .3), suggesting little effect of the experiment on the likelihood of subsequent parasitism. Nests found with more than two eggs and those that had been tested were monitored every 2-4 days until the nest failed or offspring fledged.

Playback Stimuli

We created 5-min chip or seet call playback stimuli from the audio files used in Lawson et al. (2020, 2021a). We used chip calls available through Xeno-Canto which had been recorded at sites in the U.S.A. (Colorado, Illinois, Michigan, Minnesota and Ohio) and seet calls recorded from Manitoba, Canada (from Gill & Sealy 2004). Initial construction of playback files was performed in Adobe Audition CC (Adobe, Inc., San Jose, California, 2019), with editing of files for this study completed in Audacity (Muse Group, Limassol, Cyprus, version 3.6.4). Although Northern yellow warblers do not individually recognize alarm calls (Gill & Sealy 2004), we used five unique playback files that each included calls from three randomly selected individuals to minimize pseudoreplication. Playback files had standardized call rates of 50 calls per 25 s (chip or seet) followed by 15 s of silence, repeated eight times over the 5-min sequence. Warblers show little or no response to control bird sounds (e.g. non-threatening interspecific songs and calls, see Lawson et al., 2021c); therefore, we used 5-min silent periods as controls.

We broadcast randomly selected playbacks using a JBL Flip BlueTooth speaker (JBL, Los Angeles, California, frequency range: 63Hz – 20Hz) at ~70 dB measured at 1 m distance from the speaker with an American Recorder Technology SPL-8810 sound level meter (American Recorder Technology, Simi Valley, California) set to fast response time with no weighting.

Experimental Protocol

We used a between-subjects experimental design, in which we exposed laying females to a single 5-min playback (seet or chip) or silent control (n = 33) between 0800-1300. On the day of the experiment, we positioned a CamPark T45 solar-powered remote trail camera (Campark Electronics, Shenzhen, China) and the speaker < 1 m from the nest, attaching cameras to nearby vegetation or steel u-posts, and adjusting vegetation as needed to provide a clear view of the nest. At nests receiving control treatments, we set up a trail camera to record female behavior, but did not set up speakers, such that all nests experienced some disturbance during experiments. We reasoned that setting up trail cameras presented a greater disturbance to the female than setting up the speaker because of the time involved and manipulation of vegetation to ensure a clear view of nests. We programmed trail cameras to take one photo (at 720p resolution) every 10 s from the time they were deployed to the time they were retrieved the next morning following dawn observations. We used the camera traps' internal thermometer to document ambient temperature (C) near nests.

After setting up equipment, we waited 15 min for birds to resume normal behavior before performing the experiments (Gill & Sealy, 2004). We began the playback (n = 11 chip, n = 12 seet, or n = 10 silent control) when females were off their nests and present in the area. We observed nests for 30 min following the experiments to compare female behavior captured by trail cameras with data from in-person observations. During in-person observations, we used a Zoom H4n Handy Recorder (Zoom, Hauppauge, New York, U.S.A.) for dictation to record when females entered and exited their nests, from which we quantified the total amount of time (s) females spent on the nest and the number of on/off bouts during the observation period. Due to camera malfunction at some nests, final sample sizes varied across observation periods (afternoon, n = 15; night, n = 16; dawn, n = 15).

Using the camera trap images, we quantified the proportion of photos showing female warblers at their nests and the number of on-off bouts they made during three 2-h observation periods: 1500 – 1700 ('afternoon') on the day of playback during which time female cowbirds may have prospected nests to parasitize the following day (White, 2020); 2000 – 2200, ('dusk') when female warblers decide to roost on their nests (e.g. Robins, 1971); and 0530-0730 ('dawn') the next morning when cowbird parasitism is most likely to occur (Neudorf & Sealy, 1994). Within each observation period, two observers counted the number of photos in which females were present in the nest out of the total number of photos taken from which we calculated the proportion of photos with females present. We quantified the number of on-off bouts by counting the number of times females switched between being on and off nests in successive frames. Nest camera photos from 2021 were reviewed by KVK only and photos from 2022 were reviewed by KVK and a second observer. KVK trained the second observer in data extraction, then subsequent photo review was done independently with discussion as necessary when photos were difficult to classify. Three experiments independently extracted by the second observer were checked by KVK to ensure similar counts. For these experiments, there was no difference between counts. Observers were not blinded to experimental treatment.

Statistical Analysis

We performed statistical analyses in R (version 4.1.2, R Core Team 2024) and plotted data to explore possible homogeneity of variance, violations of normality, and outliers and plotting raw data to examine potential correlations (e.g. temperature and response, time of year and response; Zuur et al., 2010). To test for differences in nest attendance within observation periods, we used two approaches. First, we ran univariate analyses on the proportion of photos of females of nests and the number of on-off bouts they

made. Next, and following Lawson et al. (2021a), we combined the proportion of photos with females on nests and number of on-off bouts using a principal component analysis on standardized variables. We used the R package "MVN" (Korkmaz et al. 2014) to scale data and check for multivariate normality.

To test the effects of playback treatments on nest attendance during each time period, we used linear models (LM) from the package "car" (Fox & Weisberg, 2019), with PC1 scores as the response variable. Ambient temperature varied with date (K Kelly, unpublished data), and we tested whether temperature affected female attentiveness by averaging temperatures measured at the beginning and end of each time period. We used model selection to determine whether temperature was needed as a covariate, employing the "AICcmodavg" package (Mazerolle 2023). The model of best fit was selected based on AICc values (difference of > 2) and parsimony when models differed by < 2. For all time periods, the best-fit models included only playback treatment as the predictor (Table S1). Post-hoc comparisons of treatment effects were performed using Tukey's HSD for pairwise comparisons of treatment types, using the glht() function from the "multcomp" package (Hothorn et al., 2008). The significance of each pairwise comparison was adjusted for multiple comparisons using the Holm method (Holm, 1979). For data visualization, we used the "effects" package (Fox & Hong, 2009) and the "ggplot2" package (Wickham, 2016).

To understand the magnitude of differences between groups (Nakagawa & Cuthill 2007), we calculated effect sizes for pairwise comparisons using the package "effectsize" (Ben-Shachar et al., 2020). We calculated using Cohen's d statistic and 95% confidence intervals, and following conventions, we interpreted values of 0.2 as small effects, 0.5 as moderate effects, and 0.8 or greater as large effects (Cohen 1988).

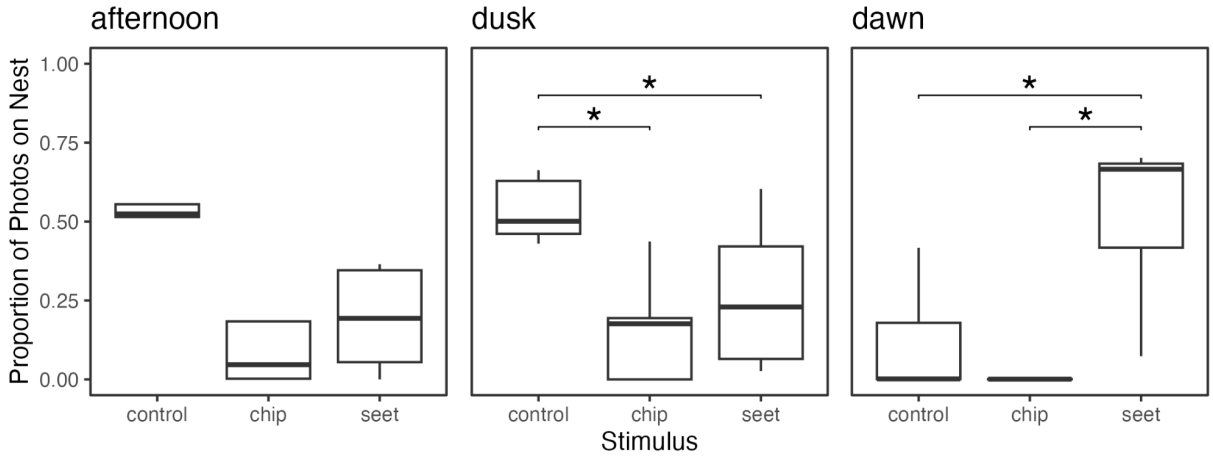
Results

For a subset of nests (n = 10), we compared trail camera footage with data from in-person observations to determine whether similar patterns of nest attendance were captured with the two methods. The proportion of camera trap photos with females on the nest was significantly positively related to the time females spent on the nest during in-person observations (Spearman ρ = 0.844, n = 10, p = .002), suggesting that equivalent data were captured by the two methods.

We observed female northern yellow warblers following 5-min playbacks of referential seet calls (n = 12), generic chip alarm calls (n = 11), or silence (n = 10) during observation periods later on the same day of treatment and the next morning (Table S2). Univariate linear model tests of the proportion of photos with females on nests revealed a significant effect of playback treatment on response during dusk (F(2,14) = 6.50, p = .01, Figure 2b) and dawn (F (2,17) = 4.96, p = .02, Figure 1), but not afternoon observations (F(2,12) = 1.43, p = .28, Figure 1). At dusk, females were at nests in a higher proportion of photos in response to control compared to seet (t(14) = 2.68, p = .045, d = 1.49, 95% CI [0.16, 2.76]) and control compared to chip (t(14) = 3.40, p = .012, d = 2.33, 95% CI [0.71, 3.89]), but there was no difference in response between seet and chip (t(14) = 0.85, p = .68, d = -0.48, 95% CI [-1.68, 0.74]). At dawn, the proportion of photos with females on nests was higher following seet playbacks compared to control (t(17) = 2.75, p = .034, d = -1.45, 95% CI [-2.59, -0.28]) and chip playbacks (t(17) = 2.65, p = .043, d = -1.59, 95% CI [-2.90, -0.22]). There was no significant difference in response between chip playback and control (t(17) = -0.22, p = .97, d = 0.12, 95% CI [-1.00, 1.23]).

Figure 1

Proportion of Photos with Female Northern Yellow Warblers at Nests Appear During Afternoon, Dusk, and Dawn Observation Periods Following Playbacks of Chip and Seet Calls, and Control Silence

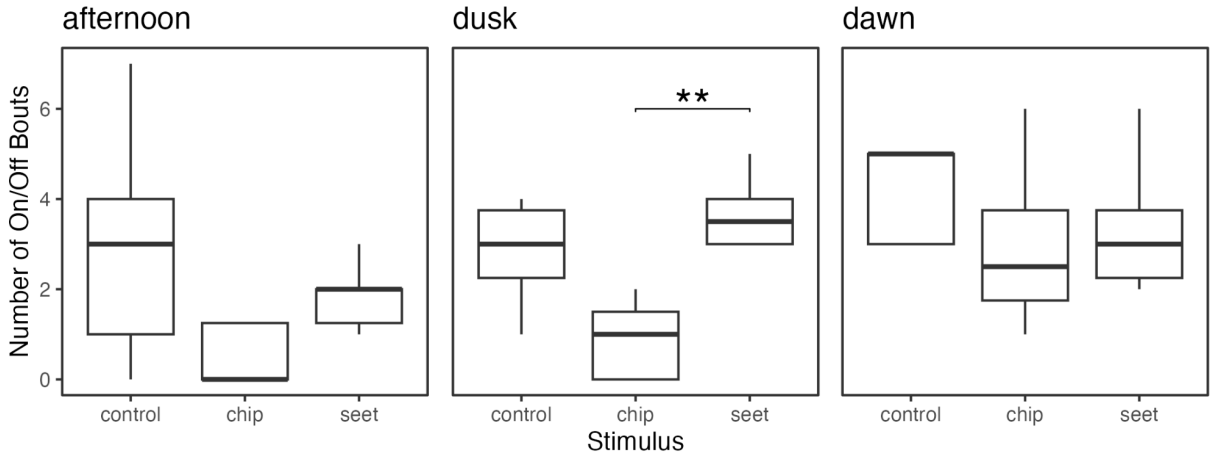


Note. Boxplots show 25th-75th interquartile range, median (line), and minimum and maximum values (whiskers). Significant pairwise *post-hoc* comparisons are shown by asterisks. Data were collected during 2-h observation periods between 1500 – 1700 ('afternoon') and 2000 – 2200, ('dusk') on the day of playback, and 0530-0730 ('dawn') the next morning.

Univariate tests of on-off bouts showed significant differences in response to playbacks at dusk ($F(2,16) = 7.54$, $p = .005$, Figure 2) but no differences in the afternoon ($F(2,14) = 0.92$, $p = .42$, Figure 2) or at dawn ($F(2,12) = 0.72$, $p = .51$, Figure 2). At dusk, females made more on-off bouts following seet playback than chip playback ($t(16) = 3.78$, $p = .005$, $d = -2.08$, 95% CI [-3.44, -0.66]), but comparisons between chip and control ($t(16) = -2.53$, $p = .05$, $d = 1.26$, 95% CI [0.03, 2.45]) and between seet and control ($t(16) = 1.20$, $p = .47$, $d = -0.83$, 95% CI [-1.99, 0.38]) were non-significant.

Figure 2

The Number of On/Off Bouts Made by Female Northern Yellow Warblers During the Afternoon, at Dusk, and at Dawn Following Playbacks of Chip and Seet Calls, and Control Silence



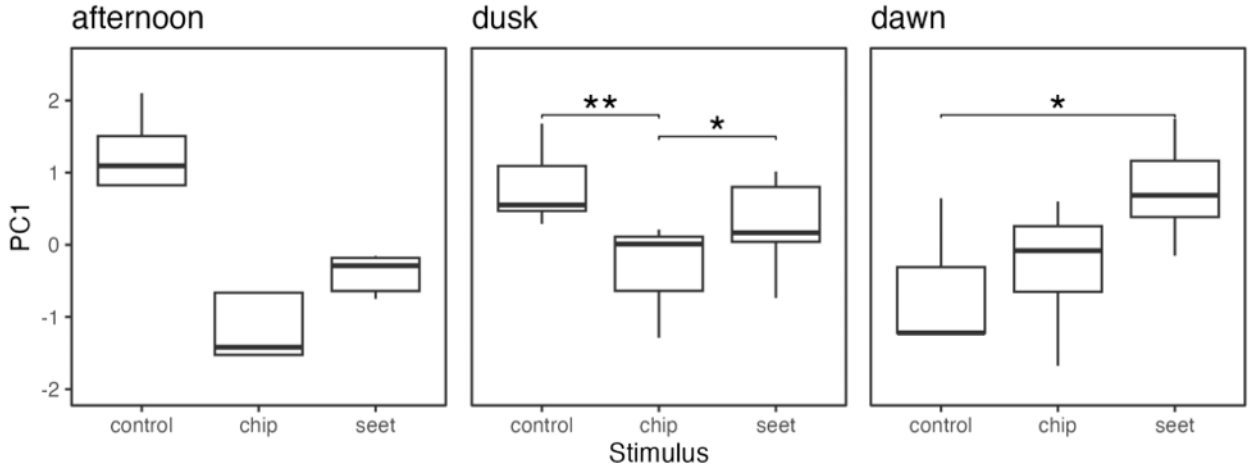
Note. Boxplots show 25th-75th interquartile range, median (line), and minimum and maximum values (whiskers). Significant pairwise *post-hoc* comparisons are shown by asterisks. Data were collected during 2-h observation periods between 1500 – 1700 ('afternoon') and 2000 – 2200, ('dusk') on the day of playback, and 0530-0730 ('dawn') the next morning.

We considered overall nest attendance by combining the proportion of photos with females on their nests and numbers of on-off bouts using PCAs for each time period. Females with more positive PC1 scores were more attentive to their nests, but the manner of attentiveness varied across observation periods. During afternoon and dusk observations, more positive PC1 scores reflect higher proportion of photos with females on nests and more on-off bouts (Afternoon PC1: loadings of both variables = 0.71, eigenvalue = 1.26, percentage variance explained = 79%; Dusk PC1: both loadings = 0.71, eigenvalue = 1.15, percentage variance explained = 66%). During dawn observations, more positive PC1 scores reveal higher proportion of photos with females on nests and fewer on-off bouts (Dawn PC1: loading for time on nest = 0.71, loading for on/off bouts = -0.71, eigenvalue = 1.00, percentage variance explained = 50%).

During afternoon observations (1500–1700, n = 15), female nest attendance was highly variable (PC1 scores ranged from 0 to 0.92) and did not statistically differ across playback treatments (F(2, 12) = 2.96, p = .090; Figure 3). Female nest attendance at dusk on the day of playback (2000–2200, n = 16) differed by treatment (Figure 3; F(2, 13) = 7.06, p = .008). *Post-hoc* comparisons and large effect sizes revealed that females spent less time on the nest and had fewer on/off bouts (PC1) following playbacks of chip calls compared to seet calls (t(13) = –2.73, p = .042, d = –1.48, 95% CI [–2.82, –0.09]) and silence (t(13) = –3.63, p = .008, d = –2.06, 95% CI [–3.61, –0.43]). PC1 values were similar for seet and control treatments (t(13) = –1.06, p = .56; d = –0.88, 95% CI [–2.11, 0.40]).

Figure 3

Nest Attendance by Female Northern Yellow Warblers During Afternoon, Dusk and Dawn Observation Periods Following Exposure to Playbacks



Note. Nest attendance (PC1) by female warblers during the afternoon, at dusk, and at dawn following playbacks of chip and seet calls, and control silence. At afternoon and dusk, more positive PC1 scores reflect more time on nests with more on/off bouts. At dawn, more positive PC1 scores reflect more time on nests but with fewer on/off bouts. Boxplots show 25th-75th interquartile range, median (line), and minimum and maximum values (whiskers). Significant pairwise *post-hoc* comparisons are shown by asterisks. Data were collected during 2-h observation periods between 1500 – 1700 ('afternoon') and 2000 – 2200, ('dusk') on the day of playback, and 0530-0730 ('dawn') the next morning.

Dawn observations include the time when female cowbirds parasitize nests. Female nest attendance at dawn the following morning (0530–0730, n = 15) differed among treatments (F(2,12) = 4.57, p = .033; Figure 3). *Post-hoc* comparison and large effect sizes showed that female warblers exposed to seet playback spent more time on their nests and left their nests less often compared to controls (t(12) = 2.89, p = .034, d = -1.90, 95% CI [-3.33, -0.40]). The *post-hoc* comparison between seet and chip playbacks did not differ statistically (t(12) = 2.04, p = .15). The effect size was large (d = -1.33), suggesting a difference in nest attendance between treatments, although the 95% CI includes zero (-2.71, 0.12). Female nest attendance

following chip and control treatments at dawn were similar with a small effect size ($t(12) = 0.65$, $p = .80$, $d = -0.39$, 95% CI [-1.71, 0.95]).

Discussion

Our study investigated whether laying female northern yellow warblers alter future nest vigilance in threat-specific ways in response to generic versus referential alarm calls. We tested whether nest attendance in the afternoon and at dusk later the same day, and at dawn the following morning differed among females depending on the type of alarm call playback. Female nest attentiveness differed depending on playback type and time of day: seet calls increased time at nests at dawn relative to chip and control, seet and chip calls decreased attentiveness at dusk relative to controls, and playbacks had no effect on female behavior around the nest in the afternoon. Our results suggest that seet calls increase nest attentiveness by female yellow warblers specifically at the time of day their nests are most likely to be parasitized by brown-headed cowbirds, whether during egg-laying (this study) or early incubation (Lawson et al., 2021a).

Alarm calls impact patterns of nest attentiveness beyond the moment of exposure in complex ways. Chip calls were associated with reduced overall nest attendance at dusk and referential seet calls associated with increased vigilance at dawn compared to controls (see also Lawson et al., 2021a). At dusk, females exposed to chip and seet calls were observed on their nests less frequently than controls and exhibited more on-off bouts compared to those exposed to seet calls or silence, with large effect sizes suggesting a disruptive effect of chip calls on attendance. At dawn, when risk of brood parasitism is highest, females exposed to seet calls were observed on nests more frequently than to chip calls or controls and their overall nest attentiveness was also higher than those exposed to controls, with intermediate response to chip playbacks. The pattern of overall nest attendance at dawn seemed less affected by females moving on and off their nests, as the number of on-off bouts at dawn did not differ by playback. Our findings support the hypothesis that laying female warblers modulate nest attendance in a threat-specific manner using acoustic cues that reflect future risk.

Referential calls produced in response to predators prompt immediate and appropriate responses suited to the type of predator encountered (Gill & Bierema, 2013; Townsend & Manser, 2013). Female northern yellow warblers produce anti-parasitic seet calls and perform nest-protection behavior when exposed to brown-headed cowbirds but not nest predators, and seet playbacks alone elicit sitting in the nest (Gill & Sealy, 1996, 2004; Hobson & Sealy, 1989). Daytime exposure to seet calls during egg-laying increased nest attendance at dawn the next day compared to controls, consistent with earlier work showing similar increased vigilance patterns during incubation (Lawson et al., 2021a). Female attendance at dawn was lower during chip than seet playback, although the effect was smaller. Thus, referential seet calls are sufficient to alter nest attendance in the future during both laying and incubation periods. Similarly, superb fairy-wrens (*Malurus cyaneus*) increased nest attendance at dawn following exposure to models of brood-parasitic shining bronze cuckoos (*Chalcites lucidus*; Feeney & Langmore, 2015). Collectively, these results suggest that females of two host species recall exposure to brood parasitic stimuli and adjust future behavior to minimize the risk of parasitism.

Alarm calls given to a variety of threats may require additional contextual information to alter behavior. Northern yellow warblers give chip calls to avian and mammalian predators, conspecifics, and non-threatening intruders (Gill & Sealy, 1996; Hobson & Sealy, 1989); nevertheless, even in the absence of contextual information, chip playbacks reduced nest attendance at dusk. These results suggest that detection of chips may alert female warblers to predation risk, seemingly resulting in a nest-avoidance response. By contrast, elevated predation risk during incubation results in increased vigilance at the nest (Martin & Briskie, 2009). Whether females perceive the calls as revealing risk to their nests or themselves is unclear. Female northern yellow warblers give higher-frequency metallic chips to taxidermic sharp-shinned hawks (*Accipiter striatus;* Gill, 1995), suggesting that females respond differently when they experience risk to themselves. Further study into the downstream effects of predation risk during early egg-laying stages in free-living passerines as well as the structure and function of chip calls and metallic chip

calls could illuminate additional perspectives on alarm calling and frontline defenses in northern yellow warblers.

The combination of referential signaling and alteration of future nest vigilance based on past exposures points to cognitive complexity in northern yellow warblers. The ability of female warblers to adjust their behavior to match perceived threats presented in the past appears consistent with expression of episodic-like memory and mental time travel (Clayton & Dickinson 1998, Dere et al. 2019). Episodic-like memory and mental time travel into the past involves the ability of individuals to recall past events and alter behavior accordingly (Dere et al., 2019), such as in food-storing animals when they recall where and when food was cached (e.g., Clayton & Dickinson, 1989). Female brown-headed cowbirds exhibit elements of mental time travel when prospecting for suitable host nests on one day, which informs their future egg-laying decisions (White, 2020). In addition, female (but not male) brown-headed cowbirds possess enlarged hippocampi, a brain region responsible for mediating spatial memory (Sherry & Guigueno, 2019). An intriguing possibility is that the cognitive abilities of brown-headed cowbirds and northern yellow warblers reflect an ongoing evolutionary arms race, in which referential calling and episodic-like memory represents 'frontline defenses' in a suite of anti-parasite defenses (Feeney et al., 2012). Additional research is needed to determine whether northern yellow warblers meet the criteria for mental time travel and to explore the cognitive plasticity of seet calling. Given evidence of alarm calls altering future behavior of females (Lawson et al., 2021a, this study), northern yellow warblers provide a suitable model for studying mental time travel in the wild.

Referential signaling through production of distinct alarm calls communicates specific threats to fitness in a variety of taxa, with the phylogenetic distribution across distantly related taxa suggesting multiple independent evolutionary origins (Gill & Bierema, 2013; Townsend & Manser, 2013). Local conditions have been hypothesized to favor the evolution of cognitive adaptations within and between species (Pravosudov, 2022). Northern yellow warblers remain the only North American bird known to use referential calls specifically for brood parasites (Gill & Bierema, 2013), despite strong natural selection by cowbirds in many wood-warbler and other host species across their range. Moreover, seet calls are rarely produced in populations allopatric with brown-headed cowbirds (Gill & Sealy, 2004; Kuehn et al., 2016), including in the related Mangrove Yellow Warbler (*Setophaga petechia*; Lawson et al., 2023) in the Galapagos Islands, Ecuador, suggesting that local adaptation to in the absence of cowbird parasitism. The study of the origin and evolution of production and perception of these calls in northern yellow warbler populations with different histories of parasitism, as well as their presence in other wood-warbler species would contribute to understanding of the ecology and evolution of animal cognition.

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Supplementary Materials

Table S1

Results of Model Selection Procedure for Nest Attendance by Female Yellow Warblers During Three Time Periods

Response	Model	K	AICc	ΔAICc	AICcWt	LL
Dawn Vigilance	**dawn.PC1 ~ treatment.type**	**4**	**45.12**	**0.6**	**0.43**	**-16.56**
	dawn.PC1 ~ treatment.type + dawn.tempavg	5	44.52	0	0.57	-13.93
Afternoon Vigilance	**afternoon.PC1 ~ treatment.type**	**4**	**54.42**	**0**	**0.13**	**-21.21**
	afternoon.PC1 ~ treatment.type + afternoon.tempavg	5	58.29	3.88	0.13	-20.81
Dusk Vigilance	**night.PC1 ~ treatment.type**	**4**	**48.63**	**0**	**0.88**	**-18.5**
	night.PC1 ~ treatment.type + night.tempavg	5	52.68	4.05	0.12	-18.34

Note. AICc values for models explaining if nest attendance at dawn differed by < 2; therefore, we selected the simplest model for subsequent analysis. For afternoon and dusk nest attendance, models with treatment only had AICc values that differed by > 2.00 from models with treatment and temperature. Selected models shown in bold. K = number of independent variables. AICc = corrected Akaike Information Criterion. ΔAICc = difference between best fit model and comparison model. AICcWt = AICc weight. LL = log-likelihood.

Table S2

Means and Standard Errors of Proportion of Photos of Females on Nests and Number of On/Off Bouts

Observation Period	Proportion of Photos on Nest		Number of On/Off Bouts		*n*
	Mean	Standard Error	Mean	Standard Error	
Afternoon	0.31	0.08	2.06	0.50	15
Dusk	0.34	0.06	2.47	0.36	17
Dawn	0.27	0.07	3.54	0.40	20